

## Chlorophyll-a in Antarctic landfast sea ice: a first synthesis of historical ice-core data

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## RESEARCH ARTICLE

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K. M. M. and M. V. contributed equally to this work.

## Key Points:

- First comprehensive collation of Antarctic landfast sea-ice core chlorophyll-*a* data established
- Algae in lowermost third of ice cores drive annual cycle of integrated biomass, but internal and surface communities are also important
- Full-profile ice-core sampling and systematic collection of auxiliary physico-chemical parameters is recommended for future studies

## Supporting Information:

- Supporting Information S1

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Chlorophyll-*a* in Antarctic Landfast Sea Ice: A First Synthesis of Historical Ice Core Data

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**Abstract** Historical sea ice core chlorophyll-*a* (Chl<sub>a</sub>) data are used to describe the seasonal, regional, and vertical distribution of ice algal biomass in Antarctic landfast sea ice. The analyses are based on the Antarctic Fast Ice Algae Chlorophyll-*a* data set, a compilation of currently available sea ice Chl<sub>a</sub> data from landfast sea ice cores collected at circum-Antarctic nearshore locations between 1970 and 2015. Ice cores were typically sampled from thermodynamically grown first-year ice and have thin snow depths (mean = 0.052 ± 0.097 m). The data set comprises 888 ice cores, including 404 full vertical profile cores. Integrated ice algal Chl<sub>a</sub> biomass (range: <0.1–219.9 mg/m<sup>2</sup>, median = 4.4 mg/m<sup>2</sup>, interquartile range = 9.9 mg/m<sup>2</sup>) peaks in late spring and shows elevated levels in autumn. The seasonal Chl<sub>a</sub> development is consistent with the current understanding of physical drivers of ice algal biomass, including the seasonal cycle of irradiance and surface temperatures driving landfast sea ice growth and melt. Landfast ice regions with reported platelet ice formation show maximum ice algal biomass. Ice algal communities in the lowermost third of the ice cores dominate integrated Chl<sub>a</sub> concentrations during most of the year, but internal and surface communities are important, particularly in winter. Through comparison of biomass estimates based on different sea ice sampling strategies, that is, analysis of full cores versus bottom-ice section sampling, we identify biases in common sampling approaches and provide recommendations for future survey programs: for example, the need to sample fast ice over its entire thickness and to measure auxiliary physicochemical parameters.

**Plain Language Summary** Antarctic sea ice is a key driver of physical, chemical, and biological processes in the Southern Ocean. Importantly, sea ice serves as a substrate for microscopic algae which grow in the bottom, interior, and surface layers of the ice. These algae are considered an important food source for Antarctic marine food webs. Using a newly collated database of historical sea ice core chlorophyll-*a* data (a proxy for ice algal biomass) from coastal sites, we describe the seasonal and vertical variability of algal biomass in Antarctic landfast sea ice. The seasonal chlorophyll-*a* development is consistent with the current understanding of physical drivers of ice algal biomass, including the seasonal cycle of irradiance and surface temperatures driving landfast sea ice growth and melt. Our analyses show that algae in the lowermost third of ice cores drive the annual cycle of integrated biomass, but internal and surface communities are also important. Through comparison of biomass estimates based on different sea ice sampling strategies, that is, analysis of full cores versus bottom-ice section sampling, we identify biases in common sampling

approaches and provide recommendations for future survey programs: for example, the need to sample fast ice over its entire thickness and to measure auxiliary physical parameters, in particular snow-thickness data.

## 1. Introduction

Landfast sea ice (fast ice) is immobile sea ice, anchored either to coasts or continental ice formations (ice shelves, glacier tongues, and grounded icebergs) or grounded over shoals (Fedotov et al., 1998; Fraser et al., 2012; Massom et al., 2001; World Meteorological Organization, 1970). Fast ice forms a narrow belt, rarely exceeding 150 km, at least off the East Antarctic coast, the only area for which detailed ice charts (Fedotov et al., 1998) and sea ice remote sensing analyses are available (Fraser et al., 2012; Giles et al., 2008).

Antarctic fast ice typically forms thermodynamically from freezing of seawater. Fast ice may also form as the result of the dynamic interception of free-drifting pack ice by coastal or icescape features and through dynamic thickening (Fraser et al., 2012; Ushio, 2006). A characteristic feature of Antarctic fast ice is the occasional presence of so-called *platelet ice*, which occurs loosely aggregated (=sub-ice platelet layer), and/or accreted (=consolidated platelet ice) beneath the fast ice (Leonard et al., 2006; Smith et al., 2001). The depth of platelet ice layers extends from a few centimeters to a few meters and is related to the proximity of ice shelves and circulating supercooled ice shelf waters (e.g., Gough et al., 2012). Current knowledge of the circum-Antarctic platelet ice distribution from coastal sites (Langhorne et al., 2015), combined with the fact that 45% of the Antarctic continental margin is associated with an ice shelf (Drewry et al., 1982), suggest an important contribution of platelet ice to Antarctic fast-ice mass budget and characteristics.

The seasonal evolution of Antarctic fast ice is shaped by the growth of ice within coastal and icescape features in winter and by the seasonal melting and mechanical breakout in summer (Fraser et al., 2012; Nihashi & Ohshima, 2015). Off the East Antarctic coastline (20–160°E, the only sector with detailed satellite analyses), fast-ice extent reaches a maximum in winter and a minimum in summer. Yet because of the greater seasonal wax and wane of pack ice, the relative contribution of fast ice to total ice extent is minimum at the overall winter sea ice maximum (approximately 4%) and maximum (approximately 19%) during the overall minimum sea ice extent in summer (Fraser et al., 2012).

Fast ice plays an important role in coastal Antarctic biogeochemical cycles and marine ecosystem function (Arrigo, 2017). It constitutes a biogeochemically active interface between the ocean and the atmosphere affecting air-ocean gas exchange (Carnat et al., 2014; Delille et al., 2007; Nomura et al., 2011; Tison, Delille, & Papadimitriou, 2017). Fast ice serves as a temporary reservoir for nutrients (de Jong et al., 2013; Grotti et al., 2005; van der Merwe et al., 2009, 2011) and controls the amount and quality of irradiance available for pelagic and sympagic primary production (McMullin et al., 2017; Perovich, 2017). Antarctic fast ice hosts some of the most productive (per volume) microalgal habitats in marine systems (Arrigo, 2014), and integrated ice algal chlorophyll-*a* (Chl*a*) standing stocks of >1,000 mg/m<sup>2</sup> have been reported (Arrigo et al., 1993). Fast-ice algal communities can contribute up to 50% to the total primary production of fast-ice covered areas (McMinn, Pankowskii, et al., 2010). The ice algal production generally occurs early in the season when water column production is low, thereby extending the productive season and damping seasonal oscillations in food supply for pelagic and benthic food webs (Kohlbach et al., 2017; McMullin et al., 2017; Swadling et al., 2000, 2004; Wing et al., 2012). Various microalgal communities from Antarctic fast ice have been described and can be classified into three main types based on their depth in the sea ice column: surface, interior, and bottom communities (Ackley et al., 1979; Arrigo, 2017; Horner et al., 1992; van Leeuwe et al., 2018). Bottom-ice communities can be further divided into interstitial ice algal communities associated with thermodynamically grown columnar ice, consolidated platelet ice layer communities, sub-ice platelet layer communities, and *strand* communities consisting of filaments that are only loosely attached to the bottom of the sea ice and are suspended into the water column (e.g., Arrigo, 2017; Arrigo et al., 1995; Grossi & Sullivan, 1985; McConville & Wetherbee, 1983).

Key environmental factors shaping the distribution and seasonality of fast-ice microalgae include light, ice temperature and related brine salinity, nutrients as well as habitable pore space (e.g., brine volume), and colonizable crystal surface area. Fast ice algal communities generally thrive in those microhabitats that provide stable environmental conditions and are most closely coupled to the under-ice water column, for example, bottom-ice layers (Arrigo, 2017). Extremely high ice algal biomass concentrations (with values

>1,000 mg Chl $a$ /m<sup>3</sup> of melted ice) have been reported for highly porous sub-ice platelet layers (Arrigo, 2017; Günther & Dieckmann, 1999; Smetacek et al., 1992).

Historically, studies on Antarctic fast ice algal communities have focused primarily on the taxonomy and physiology of algae inhabiting high-biomass microhabitats (Arrigo et al., 1995; Grossi et al., 1987; McMinn, Pankowskii, et al., 2010; Stoecker et al., 1998; Whitaker & Richardson, 1980). Time series studies have been conducted in specific regions but overall remain sparse (Carnat et al., 2014; Delille et al., 2002; Fiala et al., 2006; Günther & Dieckmann, 1999; Watanabe et al., 1990). Here we compiled a comprehensive database of ice algal Chl $a$  concentrations from Antarctic fast-ice cores collected from different regions around the continent. The data are used to (i) describe the seasonal and vertical variability of Antarctic fast-ice algal biomass and (ii) explore the relationships between this variability and environmental drivers. In addition, we compare different sampling strategies and recommend best practices for future studies.

## 2. Material and Methods

### 2.1. Data Collation

The Antarctic Fast Ice Algal Chlorophyll- $a$  (AFIAC) data set (doi:10.4225/15/589bf832b4731; available through the Australian Antarctic Data Centre) constitutes published and unpublished Chl $a$  measurements from 888 geo-referenced landfast sea ice cores, comprising 5716 individual vertical ice core sections. These were collected from 1970 to 2015 from circum-Antarctic coastal sites, clustering around eight main areas (Figure 1 and supporting information Table S1). Data were collated from peer-reviewed publications, data reports, electronic data repositories, and from individual researcher contributions. In some cases, actual data were not directly available and we used DataThief (<http://datathief.org>) to extract data from published figures. The AFIAC cores were classified according to their vertical sampling strategy (Table 1). The data set comprises ice core Chl $a$  data for *full* vertical profiles ( $\geq 3$  sections constituting the entire ice thickness), *complete* ice cores (one to two sections constituting the entire ice thickness), *intermittent* profiles ( $\geq 3$  sections, but with sampling gaps in between sections), and ice core bottom samples with a length of either 0.05 or 0.10 m referred to as *0.05-m bottom* or *0.10-m bottom*, respectively (Tables 1 and S1).

During all sampling campaigns, Chl $a$  concentrations ( $\mu\text{g/L}$ ) were determined from melted ice core sections using standard procedures, that is, melting ice samples in the dark at temperatures below 5 °C, filtration of samples on glass microfiber filters, and extraction of algal pigments with organic solvents, followed by in vitro analysis by either spectrophotometry, fluorometry (Evans et al., 1987; Holm-Hansen et al., 1965; Hoshiai, 1981), or by high-performance liquid chromatography (e.g., van Leeuwe et al., 2006; Table S1). Ice core samples were melted either with or without addition of sterile-filtered seawater (Garrison & Buck, 1986; Miller et al., 2015; Rintala et al., 2014), which does not yield significant Chl $a$  differences (Dieckmann et al., 1998).

### 2.2. Vertically Integrated Chl $a$ Content

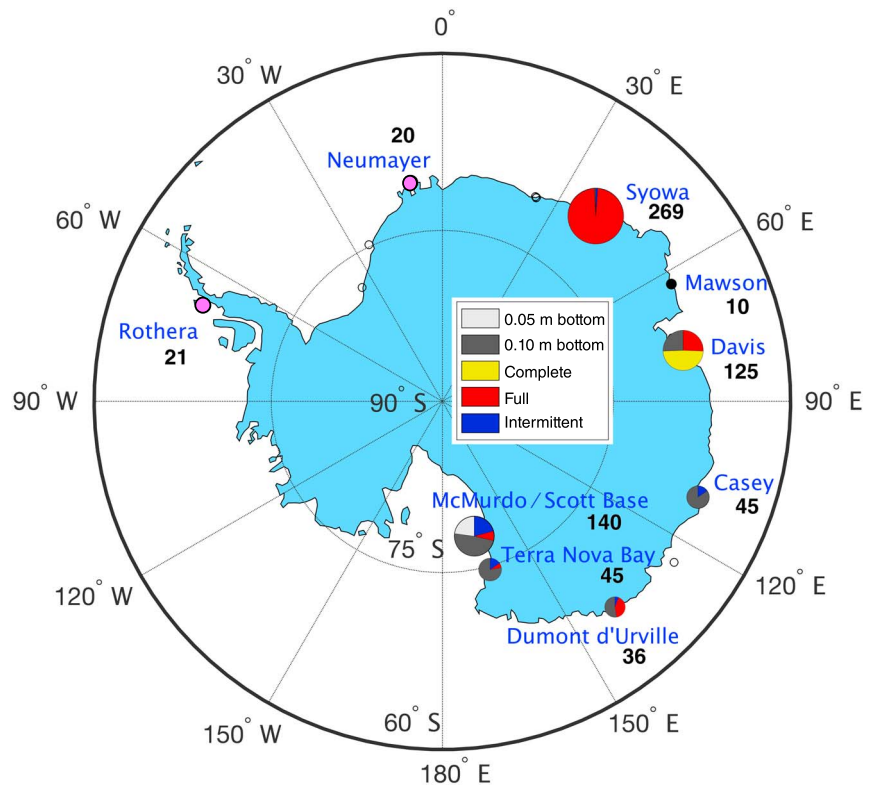
The vertically integrated Chl $a$  content ( $I_{\text{Chl}a}$ , mg/m<sup>2</sup>) is a proxy for total biomass per surface area in a sea ice core (see Meiners et al., 2012).  $I_{\text{Chl}a}$  is calculated as the sum of vertical ice core section depths multiplied by their respective Chl $a$  concentration per cubic meter of sea ice ( $C_{\text{Chl}a}$ ).  $C_{\text{Chl}a}$  (mg/m<sup>3</sup>) is the Chl $a$  concentration in meltwater ( $\mu\text{g/L}$ ) times a standard sea ice to seawater density ratio ( $917 \text{ kg/m}^3/1,020 \text{ kg/m}^3 = 0.9$ ). In addition, a *bottom biomass* ( $I_{\text{Chl}a-0.1\text{m},\text{bott}}$ ) was extracted by restricting the computation of  $I_{\text{Chl}a}$  to the few sections that cover the bottom 0.10 m of the ice cores. If a core section partly intersects the bottom 0.10 m of a core, the biomass fraction retained in the computation was equal to the depth fraction of the intersecting core section incorporated in the bottom 0.10 m.

### 2.3. Vertical Distribution

To analyze the vertical Chl $a$  distribution, all profiles were linearly interpolated (ensuring the conservation of  $I_{\text{Chl}a}$ ) on a vertical grid with three layers of equal thickness, corresponding to the surface, internal, and bottom thirds of the ice cores (Meiners et al., 2012).

### 2.4. Numerical and Statistical Analyses

Since ice core Chl $a$  data have a non-normal distribution, we mainly used non-parametric statistics for data description and analyses (i.e., medians and interquartile ranges, IQR). All database extraction and basic



**Figure 1.** Map showing sampling locations and the total number of ice cores collected at each station (black numbers). Pie chart diagrams show the number of cores grouped according to sampling strategy (for details see Table S1) at the main stations. Other sampling locations are shown as open circles (<10 cores sampled) or purple dots (10–25 cores sampled).

AFIAC data manipulations were done using the *Biogeochemical Exchange Processes at the Sea Ice Interfaces* expert group sea ice core analyzer package (Vancoppenolle, 2017).

### 2.5. Environmental Parameters

The seasonal cycle of  $I_{\text{Chl}a}$ , ice thickness ( $h_i$ , equal to ice core length) and available snow thickness ( $h_s$ ) data (from full and complete ice cores only) were analyzed in relation to meteorology and solar radiation. Mean seasonal cycles of air temperature and wind speed were derived from subdaily meteorological observations from Antarctic research stations near the main sampling areas (Syowa, Mawson, Davis, Casey, Dumont D'Urville, McMurdo, Rothera, and Neumayer; source: National Climate Data Centre, National Oceanic and Atmospheric Administration, [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)), over 1980–2016. Solar flux ( $\text{W/m}^2$ ) was derived from the formula of Shine (1984), using the latitude of each research station and restricted to cloud-free conditions because cloud fraction was unavailable.

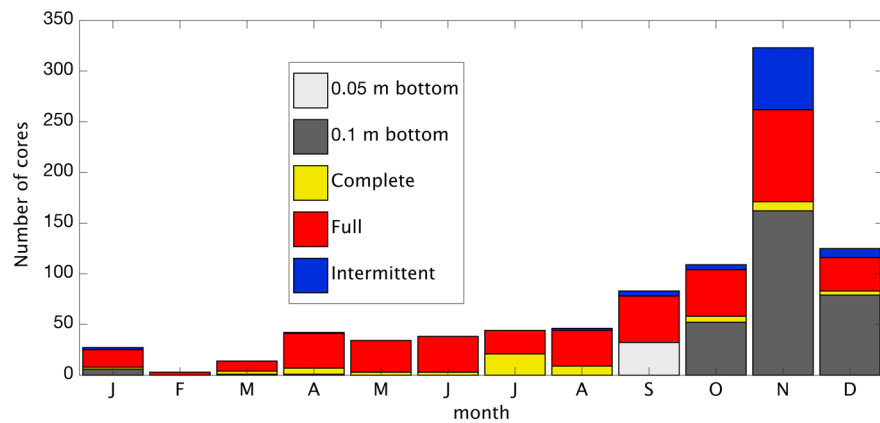
## 3. Results

### 3.1. Locations

Over the 888 AFIAC ice cores, there are 404 (46%) full cores, 66 (7%) complete ice cores, 85 (10%) intermittent cores, and 333 (37%) ice core bottom section samples with a length of either 0.05 ( $n = 32$ ; 9%) or 0.10 m ( $n = 301$ ; 91%); for details see Tables 1 and S1. Most of the ice core data originate from the East Antarctic coast (30°–180°E), and therein most samples were collected from a few distinct areas close to Antarctic research stations (Figure 1). A large fraction of the AFIAC cores ( $n = 269$ ; 30%) and the majority of full

**Table 1**  
Classification of Ice Cores According to Vertical Sampling Strategy

Sampling type category	Description
0.05-m bottom	0.05 m section from the bottom of the core
0.10-m bottom	0.10 m section from the bottom of the core
Complete	1–2 sections comprising the entire ice thickness
Full	$\geq 3$ vertical sections comprising the entire ice thickness
Intermittent	$\geq 2$ sections but with sampling gaps in between



**Figure 2.** Number of ice cores for each sampling category (described in Table 1) versus sampling month.

cores ( $n = 264$ ; 65%) were collected close to Syowa station in the Indian Ocean sector. There were only very few ice cores sampled from West Antarctica, originating from the eastern Weddell Sea (Neumayer station) and the Western Antarctic Peninsula (Rothera station). With the exception of samples from McMurdo Sound and Terra Nova Bay, the data set has a limited latitudinal range (overall range: 65.51–77.85°S; Figure 1).

The number of ice cores collected per month for each sampling category is shown in Figure 2. Most AFIAC cores were collected in austral spring, with November having the highest number of ice cores ( $n = 318$ ; 36%) of all months. The full vertical profile ice core subset has a reasonable representation with at least 30 cores for each month, except for February and March (Figure 2). February and March data were excluded from further detailed analyses because of the low number of ice cores collected in these two months. This is consistent with the timing of the overall Antarctic sea ice minimum extent when many Antarctic coastal areas have also become free of fast ice.

### 3.2. Sampling Type Distribution, Chla, and $I_{Chla}$

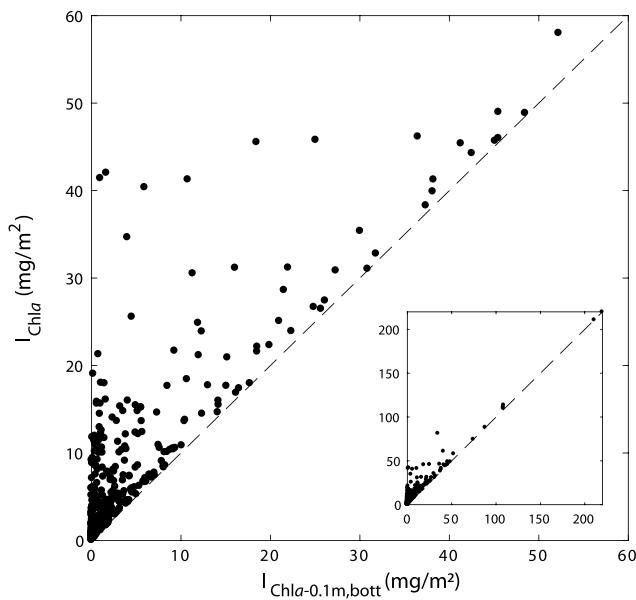
Full vertical profile cores ( $n = 404$ ) contribute 46% of all ice cores and 87% ( $n = 4975$ ) of core sections and dominate the data set. Full cores have 3–24 sections (mean = 12.3; Table 2). Intermittent ice cores comprise 3–18 sections (mean = 4.1) but cover on average only 27.5% of the total ice core length (Table 2). The different sampling categories show very different median ice core section Chla values (Table 2). Median Chla values are highest in the 0.10-m bottom category followed by the 0.05-m bottom category (originating from a single late winter study in McMurdo Sound; McMinn, Martin, & Ryan, 2010) and the complete sampling category. The full and intermittent profile ice cores show relatively low median ice core section Chla concentrations. In contrast, median integrated Chla values ( $I_{Chla}$ , mg/m<sup>2</sup>) for the different sampling categories are rather consistent, with the exception of the 0.05-m bottom category (Table 2).

**Table 2**  
Summary Statistics of the AFIAC Database

	Number of cores ( <i>n</i> )	Total number of sections (av. per core; <i>n</i> )	Core length sampled (av. per core; %)	Chla median (IQR; μg/L)	$I_{Chla}$ median (IQR; mg/m <sup>2</sup> )
All	888	5,718 (6.4)	57.8	1.5 (7.6)	4.4 (9.9)
0.05-m bottom	32	32 (1)	2.7	4.7 (5.0)	0.2 (0.2)
0.10-m bottom	301	301 (1)	6.2	50.4 (152.1)	4.5 (13.7)
Complete	66	71 (1.08)	100	4.6 (8.4)	5.2 (10.6)
Full	404	4,969 (12.3)	100	1.3 (5.7)	4.4 (9.0)
Intermittent	85	346 (4.1)	27.5	0.7 (6.9)	5.1 (9.6)

*Note.* For details on the nomenclature of sampling categories see Table 1 and text. Chla = chlorophyll-*a*, av. = average, IQR = interquartile range,  $I_{Chla}$  = chlorophyll-*a* integrated over entire core length; AFIAC = Antarctic Fast Ice Algal Chlorophyll-*a*.





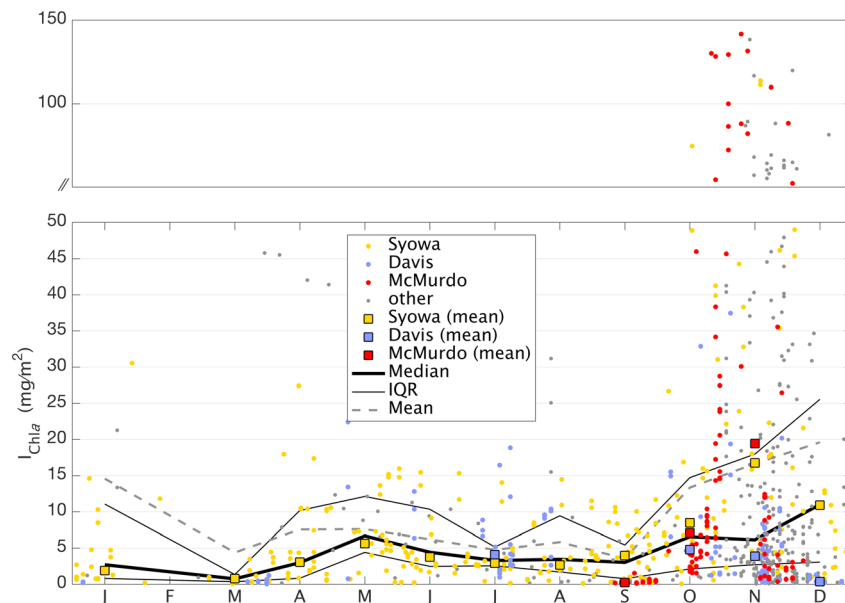
**Figure 3.** Total integrated ice algal chlorophyll-*a* standing stock ( $I_{Chla}$ ) versus chlorophyll-*a* standing stock in the lowermost 0.10 m of ice cores ( $I_{Chla-0.1m,bott}$ ), based on *Full* cores. Main figure shows data  $<60$   $\text{mg}/\text{m}^2$ . Inset: Same plot showing all data.

### 3.3. Bottom 0.1 m Biomass

Based on the full ice core data subset, the median relative contribution of the bottom 0.10 m ( $I_{Chla-0.1m,bott}$ ) to the total vertically integrated Chla ( $I_{Chla}$ ) was 41% (IQR = 61%). This contribution increases with biomass (Figure 3), reaching on average 92% for full cores with a biomass of  $>30$   $\text{mg Chla}/\text{m}^2$  (Figure 3). Thus, the biomass of ice cores with high integrated biomass, a general characteristic for the ice algal spring bloom, is dominated by bottom layers (Figure 3).

### 3.4. Seasonality of $I_{Chla}$ and Environmental Factors

Seasonal cycles of integrated ice algal biomass ( $I_{Chla}$ , range:  $<0.1$ –219.9  $\text{mg}/\text{m}^2$ , median = 4.4  $\text{mg}/\text{m}^2$ , IQR = 9.9  $\text{mg}/\text{m}^2$ ) for the main sampling areas (Syowa, Davis, and McMurdo stations) are shown in Figure 4.  $I_{Chla}$  shows a clear increase during September/October, highlighting the onset of the spring ice algal bloom with a further biomass increase into early December, followed by a rapid decline, which may be an artifact due to poor sampling coverage during January to March. A secondary annual peak in  $I_{Chla}$  occurs during late austral autumn with a maximum in May. The range of biomass values follows the medians, increasing during the peaks, and the number of low biomass values remains important during the spring bloom, which likely reflects ice algae patchiness. The highest springtime  $I_{Chla}$  values were measured in November at McMurdo Sound, with values frequently above 100  $\text{mg}/\text{m}^2$  and a monthly median of 19.4  $\text{mg}/\text{m}^2$  (IQR = 127.0  $\text{mg}/\text{m}^2$ ). In contrast, the ice cores collected near Syowa station (median = 16.7, IQR = 28.2  $\text{mg Chla}/\text{m}^2$  for November) and Davis station (median = 4.8, IQR = 7.7  $\text{mg Chla}/\text{m}^2$  for October) had generally lower biomass maxima.



**Figure 4.** Seasonal evolution of ice algal biomass ( $I_{Chla}$ ,  $\text{mg Chla}/\text{m}^2$ ) from various subsamples of the AFIAC data set. Dots depict values from the 888 individual cores. The three main sampling locations are colored (Syowa, Davis, and McMurdo), whereas gray symbols refer to all other locations. Thick and thin solid lines: Monthly median and interquartile range for *full*, *complete*, and *intermittent* cores only (for details of sampling categories see text). Dashed gray line gives the monthly mean biomass from the same cores. Squares give the monthly median biomass at the three main sampling locations, depicted only where at least 10 cores contribute to the median and regardless of the sampling method. AFIAC = Antarctic Fast Ice Algal Chlorophyll-*a*.

Ice thickness ( $h_i$ ; Figure 5a) increased from March to October, followed by a phase of slow decline until January, in a relative consistent manner across the different sampling areas. McMurdo ice cores collected in spring were among the thickest in the data set. Syowa station ice cores sampled in autumn were frequently  $>1$  m long. Snow depth data are available for 511 AFIAC ice cores. The data do not allow the discrimination of any seasonal signals in snow depth (Figure 5b). It is notable that snow depths were 0 for the majority of measurements ( $n = 299$ , i.e., 57.1% of the snow data, range: 0–0.67 m, median = 0 m, IQR = 0.075 m). This is mostly due to contributions from Davis ( $n = 123$ ) and McMurdo ( $n = 134$ ) cores, where the median reported snow depths were 0 m as well. Both stations are associated with possible minima of snow accumulation, according to ERA-interim reanalysis data (Maksym & Markus, 2008). There is a tendency for deeper snow toward West Antarctica, with the three westernmost stations having the thickest snow depth of the data set: Rothera (median = 0.10 m, IQR = 0.10 m,  $n = 20$ ), Neumayer (median = 0.19 m, IQR = 0.16 m,  $n = 19$ ), and Syowa (median = 0.13 m, IQR = 0.12 m,  $n = 27$ ). All other stations with available data had a median snow depth well below 0.10 m.

Due to their similar latitude, most stations are comparable in terms of (clear sky) solar radiation (Figure 5c). The exception is McMurdo, which experiences the return of sunlight about a month later than the other stations. Annual mean air temperatures (Figure 5d) were the lowest at McMurdo ( $-16.6$  °C) and Neumayer ( $-16$  °C) and highest at Rothera ( $-3.8$  °C). Wind speed (Figure 5e) had relatively small changes across the annual cycle but is highly variable among the different sampling areas, likely due to varying exposure to prevailing winds. McMurdo data (5.0 m/s) and Syowa station data (6.8 m/s) had the weakest annual average winds, whereas Mawson station had the highest average wind speed (11.8 m/s).

### 3.5. Vertical Chla Distribution

To analyze the vertical Chla distribution, all full profiles were interpolated on a three-layer vertical grid. This grid was used to describe the seasonal ice algal distribution and development in the upper, middle, and lower third (=surface, internal, and bottom) of the full ice core category. The seasonal development of integrated Chla for these three layers (monthly mean) and total  $I_{Chla}$  is shown in Figure 6a. Total integrated biomass ranges between  $<0.1$  and  $219.9$  mg Chla/m<sup>2</sup> (median =  $4.4$  mg Chla/m<sup>2</sup>, IQR = 9.0; Table 2). It shows a strong increase during austral spring (September to November) and peaks in December (Figure 6a). There is also a pronounced secondary peak in  $I_{Chla}$  in May. This autumn peak is mostly driven by observations from newly grown ice from Syowa station and cannot be considered as an artifact of the low amount of data in February and March. Yet the lack of data from March makes the identification of the exact timing of the fast ice algal autumn peak problematic. This autumn ice algal peak is vertically more uniform, for example, showing contributions from both bottom layers and interior layers, when compared to  $I_{Chla}$  during spring, which is dominated by bottom-ice algae.

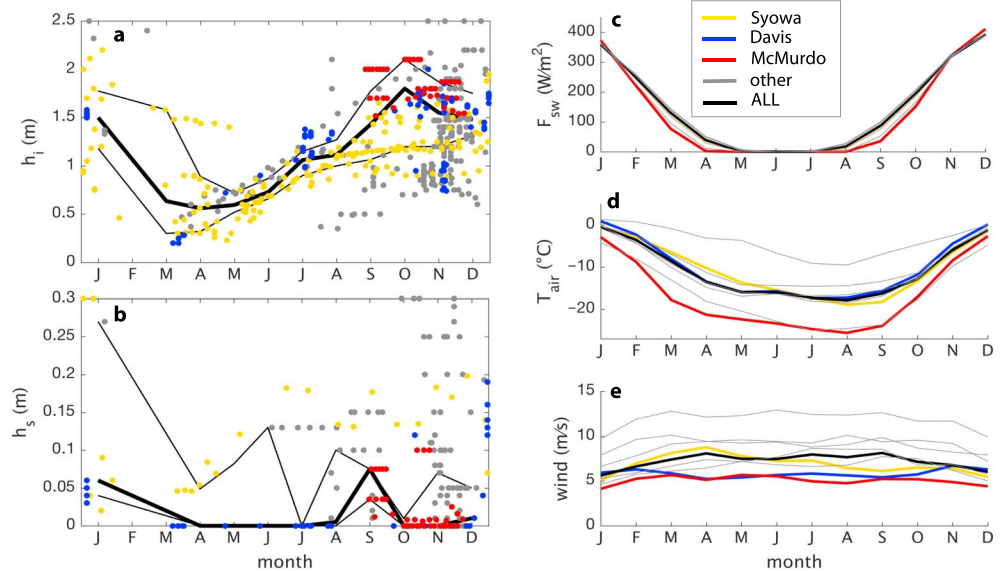
The biomass in the lowermost third of the ice cores dominates integrated biomass except during winter and very early spring, when overall biomass is very low (Figure 6b). Algal communities in the interior third of the ice increase in late autumn and in summer and dominate  $I_{Chla}$  between June and September, that is, during the ice growth season (Figure 5b). The surface algal communities exhibit relatively low Chla values, which show a slight increase during summer. Surface communities never dominate  $I_{Chla}$  but show noteworthy relative contributions during times of very low  $I_{Chla}$ , that is, during winter, and also during late summer (Figure 6b).

## 4. Discussion

### 4.1. Limitations of the Data Set

Our study provides the first quantitative circumpolar synthesis of Chla concentrations in Antarctic fast ice. AFIAC constitutes a significant extension of an existing Antarctic pack ice Chla data collation (ASPeCt-Bio data set; Meiners et al., 2012). Limitations of the AFIAC data set are related to unavoidable biases associated with using Chla as a proxy for ice algal biomass (Meiners et al., 2012) and more generally with biases related to Antarctic fieldwork and ice core sampling. The data are not uniformly distributed across seasons, regions, or ice types. The data set is temporally biased toward springtime (October–December) and spatially biased toward East Antarctica, with a large number of samples originating from the Indian Ocean sector, in particular from Syowa station.

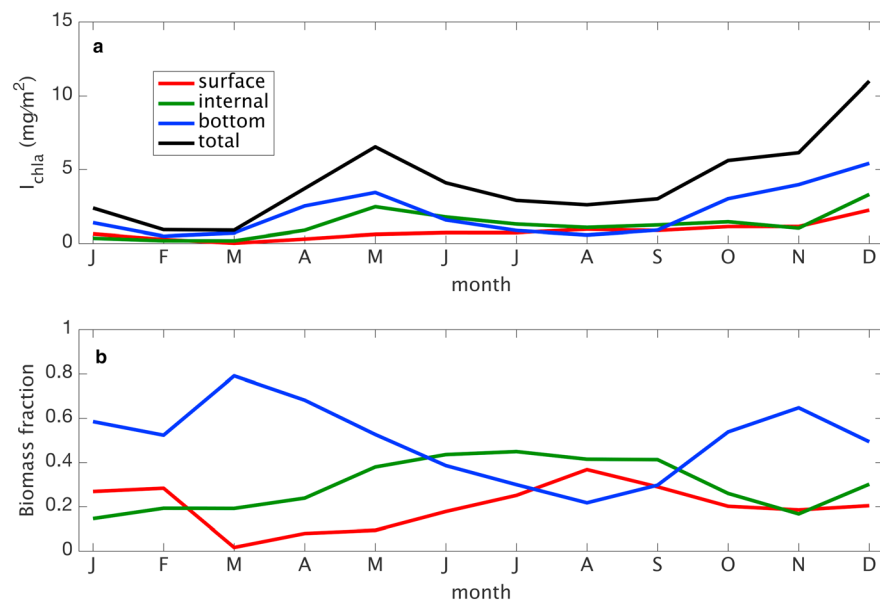




**Figure 5.** Seasonal cycles of the main environmental parameters: (a) ice thickness ( $h_i$ ) and (b) snow depth ( $h_s$ ), (c) incident clear-sky solar flux, (d) air temperature, and (e) wind speed for the main AFIAC sampling areas (Syowa, Mawson, Davis, Casey, Dumont d'Urville, McMurdo, Rothera, and Neumayer). Colored symbols and lines depict observations from the three main stations (Syowa, Davis, and McMurdo); gray symbols refer to all other locations. Black lines indicate monthly medians (thick) and interquartile ranges (thin). Air temperature and wind speed data are from automated weather research stations (National Climate Data Centre, National Oceanic and Atmospheric Administration, [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)). Clear-sky solar flux is derived from the formula of Shine (1984), using the latitude of each station. AFIAC = Antarctic Fast Ice Algal Chlorophyll-*a*.

#### 4.2. Ice Core Sampling Biases

While ice-coring techniques are well suited to sample interstitial communities within consolidated sea ice, they are insufficient for quantitative sampling of sub-ice platelet ice communities as well as strand communities consisting of algal filaments that are only loosely attached to the subsurface of the ice. Both community



**Figure 6.** Monthly median time series of (a) vertically integrated chlorophyll-*a*, and (b) percentage fraction of vertically integrated chlorophyll-*a* for the upper third (surface), the interior third (internal), and bottom third (bottom) of ice cores (calculated from the fully vertically resolved cores [full,  $n = 404$ ] only).

types are found in association with Antarctic fast ice (Arrigo, 2017; Arrigo et al., 1995; McConville & Wetherbee, 1983). Sub-ice platelet ice layers that become consolidated into fast ice sheets remain brittle, and material from these layers is typically lost during ice core sampling. Due to the lack of ancillary data, such as descriptions of ice crystal structure to identify consolidated platelet ice, or information on the occurrence of algal filaments and sub-ice platelet layers, we were unable to investigate and properly quantify Chl *a* concentrations within specific ice growth types. We note that algal communities in these specific ice types can significantly contribute and dominate ice-associated algal biomass in some Antarctic fast ice areas (Arrigo, 2017; Arrigo et al., 1995; Dieckmann et al., 1992; McConville et al., 1985). Thus, the AFIAC samples provide a conservative estimate of the total amount of ice-associated algal biomass in Antarctic fast ice, in particular for areas affected by platelet ice, for example, areas in close proximity to an ice shelf, or for fast ice harboring ice algal strand communities. The prevalence of these different community types in different areas is considered a key driver of the regional variability of Antarctic landfast sea ice algal biomass (e.g., Wongpan et al., 2018).

#### 4.3. Spatial Variability

The large dispersion of AFIAC biomass data, in particular during the spring bloom, emphasizes the high spatial variability in ice algal distribution which has been reported previously (e.g., Eicken et al., 1991; Lange et al., 2017). Conducting time series sampling of fast-ice algal communities in the Canadian Arctic, Welch and Bergmann (1989) were able to predict ice algal biomass from date and snow thickness, that is, accumulated light exposure. They suggested that biomass spatial variability is driven by a *head start* phenomenon, for example, between-site differences in biomass resulting from differences in early-season snow cover are maintained, and potentially amplified, throughout the growth season. Antarctic ice algal spatial variability has been attributed to a variety of environmental parameters including water column properties at the time of ice formation, sea ice growth history and ice crystal texture, ice thickness and snow depth, and surface flooding (Arrigo, 2017; Meiners et al., 2017). The dispersion of the AFIAC biomass data may thus reflect interannual variation in these physical properties, particularly in ice age and snow thickness affecting head start growth. Indeed, fast ice, and in particular offshore areas, can be subject to frequent mechanical sea ice breakout controlling the age of the fast ice and thereby affecting total ice algal biomass as well as its vertical distribution. Fast-ice breakout frequency is itself controlled by icescape features such as grounded icebergs as well as glacier tongue dynamics and storm events (Fraser et al., 2012; Massom et al., 2001), which are subject to interannual variation and thus may indirectly drive interannual variability of ice algal biomass at a particular location (Remy et al., 2008).

Furthermore, other more time-invariant factors such as water depth, bottom topography, and the proximity of ice shelves will affect under-ice currents and thus regional nutrient availability, thereby influencing ice algal biomass distributions. Tidal currents, for example, have been correlated with biomass responses in Arctic fast ice (Cota et al., 1987; Cota & Horne, 1989; Gosselin et al., 1985), with ocean ice tidal shear inducing exchange of nutrient-depleted brine with nutrient-replete under-ice water due to forced convection (Feltham et al., 2002; Vancoppenolle et al., 2013). McMinn et al. (2000) reported increased photosynthesis in an Antarctic fast-ice algal bottom community exposed to increased under-ice current flow. Evidently, a single ice core or a small number of ice cores collected from a single site will not necessarily provide representative data for a particular season or region (e.g., Lange et al., 2016; Meiners et al., 2017).

#### 4.4. AFIAC Physical Characteristics and Drivers of Chl *a* Seasonal Development

The physical characteristics of the fast-ice environment such as the seasonal increase and decrease in fast-ice thickness associated with an overall low variance are well represented within the data set. The AFIAC ice thickness data show a gradual increase from April to October and a strong decline during austral summer, thereby resembling a full annual ice growth cycle. This pattern in thickness evolution suggests that AFIAC is dominated by thermodynamically grown first-year fast ice, for the following three reasons: (1) There are not many thick ice cores at the beginning and end of the ice season, which would indicate the presence of a significant contribution of multiyear sea ice in the data set; (2) most of the AFIAC cores were collected in close proximity to research stations, that is, from nearshore sites, which suggests thermodynamic rather than dynamic ice growth conditions and a relative low breakout frequency (Fraser et al., 2012); and (3) the median AFIAC ice thickness (median = 1.38 m, IQR = 0.82 m, February and March excluded) is consistent with a maximum (end of the growth season) thermodynamic thickness of 1.5–2.0 m reported for Antarctic fast ice

(Heil et al., 1996). However, we note that sea ice off Syowa station, that is, in Lützow-Holm Bay, features a high proportion of multiyear landfast sea ice (Fraser et al., 2012; Hoshiai, 1972) and that some AFIAC cores from this area possibly represent multiyear landfast sea ice cores (Watanabe et al., 1990). We also note that the AFIAC data set shows a higher overall mean ice thickness and lower ice thickness variability when compared to Antarctic pack ice, which is subject to ice motion and deformation (Meiners et al., 2012; Worby et al., 2008).

Snow is a key driver of ice algal dynamics as it strongly controls light availability for ice algal communities (Mundy et al., 2005; Perovich, 2017). In Antarctic fast ice environments snow limits algal growth, and generally inverse correlations between snow thickness and ice algal biomass have been reported (Ackley & Sullivan, 1994; Grossi et al., 1987; Grossi & Sullivan, 1985; Vermeulen, 2013). Recent studies and reviews on Arctic fast ice have shown a seasonally changing influence of snow cover on ice algal bottom communities (Campbell et al., 2015; Lange et al., 2015; Mundy et al., 2005) and demonstrated how snow dynamics can alter the timing, duration, and magnitude of ice algal spring blooms (Leu et al., 2015). Recent Antarctic studies have highlighted the importance of snow loading for algal biomass accumulation in pack ice during winter and spring (Meiners et al., 2017; Tison, Schwegmann, et al., 2017), but the role of snow in driving Antarctic fast ice algal dynamics remains poorly understood. Snow depth data were available for 57.4% of the AFIAC sites and showed relative low variability, including a very high number of zero snow depth sites ( $n = 299$ , 57.1% of all snow measurements). Accumulation of snow on sea ice is controlled by precipitation as well as snow redistribution that can result in an increase as well as a decrease in localized snow depths. We attribute the low snow depths in the AFIAC data set to the dominance of McMurdo/Scott Base and Davis stations, which are characterized by very low snow accumulation, and also to the exposure of coastal fast ice to katabatic winds exporting snow to more offshore locations (Sturm & Massom, 2017). The high number of zero snow depth measurements indicates wind scouring but may also present a sampling bias, for example, preferred sampling of undeformed and snow-free ice by research teams. Overall, the mean AFIAC snow thickness ( $0.052 \pm 0.098$  m) is much thinner than more comprehensive snow thickness observations for Antarctic pack ice (e.g., ASPeCt climatology for snow thickness:  $0.16 \pm 0.20$  m, Worby et al., 2008), which is typically less influenced by strong coastal winds (e.g., Massom et al., 2001) and likely experiences higher precipitation due to the vicinity of the open ocean. Assuming that the low overall snow depth in the AFIAC data set is characteristic for nearshore Antarctic fast ice, we hypothesize that this ice type provides higher light availability for ice algae when compared to Antarctic pack ice.

#### 4.5. Ice Algal Chla

Integrated Chla concentrations ( $I_{\text{Chla}}$ ) reported in AFIAC (median = 4.4, IQR = 9.9 mg/m<sup>2</sup>; Table 2) are expectedly lower than the median value (43 mg/m<sup>2</sup>) of a compilation of maximum Chla standing stocks for Antarctic sea ice associated communities, which includes high biomass values for platelet ice, strand and pack ice surface assemblages (Arrigo, 2017, and references therein). In the AFIAC data set, ice cores collected in McMurdo Sound during spring show most of the highest  $I_{\text{Chla}}$  values (Figure 4). We attribute this to the low snow cover measured for these samples, but in particular to the occurrence of consolidated platelet ice layers in this area. Due to a lack of ice structural data, we cannot test this hypothesis; nevertheless, platelet ice is widespread in this area, and very high biomass values have been reported for ice algal assemblages growing at the interface of the sea ice bottom and the sub-ice platelet layers in McMurdo Sound during spring (Arrigo et al., 1995; Grossi et al., 1987). Under-ice platelet layers have also been reported from sea ice off Neumayer station but are generally lacking from the Australian stations Davis, Casey, and Mawson (Günther & Dieckmann, 1999; Heil & Allison, 2002; Langhorne et al., 2015). The overall AFIAC median  $I_{\text{Chla}}$  (4.4 mg/m<sup>2</sup>, IQR = 9.9 mg/m<sup>2</sup>) is slightly higher than the median integrated Chla concentration for Antarctic pack ice (3.0 mg/m<sup>2</sup>, IQR = 6.8 mg/m<sup>2</sup>) calculated from the ASPeCt-Bio compilation using the same equations as applied in this study (Meiners et al., 2012). We consider this slightly elevated  $I_{\text{Chla}}$  in fast ice as a likely result of increased light availability (as discussed above) as well as increased nutrient supply and storage in Antarctic coastal sea ice environments (Fripiat et al., 2015; Grotti et al., 2005). High nutrient accumulation has been observed in Antarctic fast ice (Arrigo et al., 1995; Fripiat et al., 2015; Günther et al., 1999; Lannuzel et al., 2014), and supply for ice algal communities is likely enhanced through forced brine convection due to stronger under-ice tidal currents when compared to the pack ice regime (Vancoppenolle et al., 2013). In addition, grazing pressure may have contributed to the observed difference in ice algal biomass accumulation between Antarctic fast and pack ice but remains difficult to quantify. However,

thermodynamically grown fast ice with a columnar ice crystal texture may be particularly inaccessible for larger heterotrophic grazers (Arrigo et al., 2014; Krembs et al., 2000). Nevertheless, Antarctic ice algal carbon contributes significantly to the diet of krill residing at the ice-water interface of pack ice (e.g., Kohlbach et al., 2017, 2018; Schaafsma et al., 2017; Schmidt et al., 2018), and thus the importance of grazing needs further clarification. In conclusion, the observed differences in biomass accumulation in fast ice versus pack ice are consistent with various sea ice physicochemical as well as biological factors, while the relative importance of the factors remains poorly understood.

#### 4.6. Seasonal Development of $I_{Chla}$

In contrast to phytoplankton biomass, ice algal biomass cannot be observed with remote sensing techniques and in situ time series measurements remain the only way to observe seasonal and annual ice algal dynamics (Leu et al., 2015). In this study we combine circumpolar data from snapshot measurements, short-to-medium length campaigns (weeks to months), and a limited number of full-season time series (Delille et al., 2002; Günther & Dieckmann, 1999; Watanabe et al., 1990; Table S1) to construct an annual cycle of Antarctic fast-ice algal biomass. In this cycle,  $I_{Chla}$  shows a maximum during early summer following a strong increase between September and December. The increase in median  $I_{Chla}$  occurs in October in the AFIAC fast-ice data set, whereas the increase occurs in September in the ASPeCt-Bio pack ice data set (Meiners et al., 2012). The timing of the spring ice algal bloom therefore appears to be dependent on station latitude, noting that monthly median values are influenced by sampling effort. In the AFIAC data set, the first biomass increase is detected in September at Syowa, whereas the main increase occurs in October at the McMurdo Sound sites. The overall median of  $I_{Chla}$  tends to follow the McMurdo data, which dominate at that time of the year. The difference in bloom onset between Syowa and McMurdo is likely due to latitude-driven differences in insolation. Syowa station is located at 69°S, whereas McMurdo is at about 77°S, which results in a notable delay in the end of the polar night (22 August for Syowa, 16 September for McMurdo; see Figure 5c). A similar latitudinal dependency of the onset of the ice algal bloom has been observed in simulations of Arctic pack ice algal dynamics (Castellani et al., 2017). The AFIAC annual Chla cycle shows a secondary peak in May characteristic for an austral autumn ice algal bloom (Hoshiai, 1977). The decrease of ice algal biomass in summer is associated with an overall thinning of the ice cover and can thus be attributed to ablation of bottom ice algal communities (Figure 6). Furthermore, nutrient limitation may contribute to the decline in ice algal biomass (McMinn et al., 1999; Meiners & Michel, 2017; Robinson et al., 1998).

#### 4.7. Vertical Distribution of Chla

During the ice algal growth season (September to May) total integrated biomass is dominated by bottom ice algal communities. These communities mainly consist of pennate diatom species (van Leeuwe et al., 2018). We note that the biomass peak in autumn is vertically more uniform than the ice algal accumulation during spring. This can be attributed to an overall thinner ice thickness and the potential incorporation of remnant phytoplankton cells into the newly forming sea ice (e.g., Meiners & Michel, 2017). In addition, autumn surface cooling induces vertical brine convection and thus supports growth of interior ice algal communities before increasingly harsh conditions, including decreasing irradiance, colder ice temperatures, and increasing brine salinities, will limit algae growth within the sea ice interior. Ice algal growth in sea ice interior layers may also be supported through sustained algal photosynthesis due to higher light availability in these layers when compared to bottom-ice layers. During winter (July to September) the highest ice algal Chla fraction is found in the sea ice interior. This may be the result of autumnal ice accretion that traps bottom-ice communities; that is, interior algal biomass peaks are likely to resemble residual autumn ice algal blooms that got incorporated into the ice interior due to ice growth over autumn and winter (Grossi & Sullivan, 1985; Günther & Dieckmann, 1999; van Leeuwe et al., 2018). The presence or absence of interior biomass peaks may be attributed to fast-ice breakout frequency (McConville & Wetherbee, 1983). As winter-reforming ice contains less biomass than autumnal ice (Niemi et al., 2011), increase of breakout frequency likely decreases overall Chla biomass. We consider the dominance of the interior biomass fraction during winter as a specific feature of nearshore ice core samples, which may not be found in offshore, less stable, landfast sea ice regions. We hypothesize that internal communities in undeformed sea ice with low snow cover form as a result of rapid bottom-ice accretion. In this case the ice algal community cannot reposition to the ice-water interface through vertical migration (Aumack et al., 2014) and gets trapped in sea ice interior layers. On the other hand, in snow-covered sea ice, surface flooding inducing warm and permeable conditions is an alternative

mechanism for the establishment of internal Chl*a* maxima (e.g., Meiners et al., 2017; Tison, Schwegmann, et al., 2017).

Integrated Chl*a* concentrations in the upper third of the AFIAC cores were low throughout the year except for early summer (November to December) when ice algal biomass in surface layers showed a small increase. While surface algal communities are characteristic for Antarctic pack ice, for example, due to snow loading and subsequent surface flooding (Arrigo, 2014; Meiners et al., 2012, 2017), they are less pronounced in landfast sea ice. Sea ice surface algal communities are dominated by flagellate species and generally occur when environmental conditions ameliorate during summer, for example, when ice temperatures increase and brine salinities decrease (van Leeuwe et al., 2018, and references therein). Stoecker et al. (1998) described the succession of a halo- and cryo-tolerant flagellate-dominated community developing into a diatom-dominated community in snow-free landfast sea ice in McMurdo Sound. In contrast, Whitaker and Richardson (1980) reported on a surface diatom community associated with near-shore, snow-covered, and surface-flooded landfast sea ice affected by tide cracks. The observed vertical zonation of Chl*a* in AFIAC is consistent with the seasonal dynamics of the major environmental drivers and likely additionally affected by small- and medium-scale sea ice physical features. The algal communities particularly thrive in layers that are spatially or temporally most coupled to the water column, supplying nutrients and providing seed populations of microalgae (Arrigo, 2017; van Leeuwe et al., 2018). We note that our description of the drivers of the seasonal and vertical distribution of Chl*a* is specific for thermodynamically grown landfast sea ice. Recent work by Lieser et al. (2015) and DeJong et al. (2018) provide evidence for the occurrence of frazil-ice associated algal blooms in offshore ice production areas of the Southern Ocean during late summer/early autumn. These blooms develop under much more dynamic conditions; that is, they are ultimately stimulated by strong winds (DeJong et al., 2017).

#### 4.8. Sampling Strategies

Our analyses allow the evaluation of different sea ice sampling strategies, that is, analysis of full cores, intermittent cores, and bottom-ice section sampling, and indicate that classical and prevailing sampling strategies focusing on bottom communities are associated with shortcomings. Given the strong vertical gradients in Antarctic fast-ice Chl*a* concentrations, the sampling resolution has a strong impact on volumetric algal pigment estimates (median values of sampling categories; Table 2). Our study shows that bottom-ice section sampling severely underestimates chlorophyll biomass integrated over the entire ice thickness, except for very high biomass regimes during spring. For future studies of Antarctic fast-ice algae, we recommend at least weekly sampling of fully vertically resolved ice cores consisting of a minimum of three to four ice core sections to support accurate chlorophyll biomass estimates and support the AFIAC database. There is also a strong need to develop new sampling methods to accurately determine ice algal biomass in platelet ice layers and in strand communities. Emerging noninvasive bio-optical methods may help in this respect (e.g., Cimoli et al., 2018; Wongpan et al., 2018) but will need to be cross-calibrated with methods that allow the collection of discrete samples for *in vitro* determination of biomass from fragile and highly porous ice environments (e.g., suction and slurp guns; Miller et al., 2015, and citations therein). Furthermore, the spatial variability of Chl*a* in fast ice is probably not well represented by sampling a limited number of ice cores. In Arctic pack ice, ice algal biomass was significantly underestimated by ice core-based sampling compared to under-ice profilers measuring ice algae biomass at high resolution over hundreds of meters to kilometers of distance (Lange et al., 2016, 2017). The spatial variability of ice algae biomass is often controlled by physical drivers, such as snow thickness and sea ice structure. Therefore, biological sea ice sampling should quantify spatial variability and include concomitant measurements of sea ice physical properties (Miller et al., 2015). In particular, there is a considerable lack of snow data and ice structural information that would help to better understand the role of key physical drivers in Antarctic fast-ice algal dynamics. Fast-ice studies should be extended to the West Antarctic sector and more offshore regions focusing on areas with different breakout frequencies to tease out links between fast-ice cover duration and ice algal biomass accumulation. We further recommend increasing long-term observations that capture the full annual cycle of fast-ice growth and decay. The development of automated ice-tethered observatories that combine physical (Heil et al., 2011; Nicolaus et al., 2010) and biological (Campbell et al., 2014, 2015; Lange et al., 2016, 2017; Meiners et al., 2017; Melbourne-Thomas et al., 2015) sea ice measurements may become key in furthering our understanding of ice algal dynamics and its physical controls in Antarctic fast ice. As atmospheric conditions are key



drivers of fast-ice algal dynamics, research teams should increase the use of meteorological data collected at nearby coastal stations to support their data interpretation. Given the importance of snow as a driver of fast-ice ecosystems, fast-ice snow surveys need to be incorporated into monitoring programs at Antarctic research stations.

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#### 5. Concluding Remarks

Our study provides the first quantitative circumpolar synthesis of the seasonal cycle of Chl<sub>a</sub> concentrations in Antarctic fast ice. Our investigation demonstrates the seasonally varying contribution of surface, internal, and bottom sea ice communities to *I*<sub>Chl<sub>a</sub></sub>. Ice algal communities in the lowermost third of the ice cores dominate Chl<sub>a</sub> concentrations during most of the year, but internal and surface communities are important, particularly during seasons with low overall biomass. Our analyses indicate the strong influence of environmental drivers on integrated ice algal biomass but highlight the lack of detailed concomitant sea ice physical as well as chemical data (snow depth, ice structure and other physical properties, and nutrients).

#### References

- Ackley, S. F., Buck, K. R., & Taguchi, S. (1979). Standing crop of algae in the sea ice of the Weddell Sea region. *Deep Sea Research Part A. Oceanographic Research Papers*, 26(3), 269–281. [https://doi.org/10.1016/0198-0149\(79\)90024-4](https://doi.org/10.1016/0198-0149(79)90024-4)
- Ackley, S. F., & Sullivan, C. W. (1994). Physical controls on the development and characteristics of Antarctic sea ice biological communities—A review and synthesis. *Deep Sea Research Part I: Oceanographic Research Papers*, 41(10), 1583–1604. [https://doi.org/10.1016/0967-0637\(94\)90062-0](https://doi.org/10.1016/0967-0637(94)90062-0)
- Arrigo, K. R. (2014). Sea ice ecosystems. *Annual Review of Marine Science*, 6(1), 439–467. <https://doi.org/10.1146/annurev-marine-010213135103>
- Arrigo, K. R. (2017). Sea ice as a habitat for primary producers. In D. N. Thomas (Ed.), *Sea ice*, (pp. 352–369). Hoboken, NJ: John Wiley. <https://doi.org/10.1002/9781118778371.ch14>
- Arrigo, K. R., Dieckmann, G., Gosselin, M., Robinson, D. H., Fritsen, C. H., & Sullivan, C. W. (1995). High resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: Biomass, nutrient, and production profiles within a dense microalgal bloom. *Marine Ecology Progress Series*, 127, 255–268. <https://doi.org/10.3354/meps127255>
- Arrigo, K. R., Robinson, D. H., & Sullivan, C. W. (1993). High resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: Photosynthetic and biooptical characteristics of a dense microalgal bloom. *Marine Ecology Progress Series*, 98, 173–185. <https://doi.org/10.3354/meps098173>
- Aumack, C. F., Juhl, A. R., & Krembs, C. (2014). Diatom vertical migration within land-fast Arctic sea ice. *Journal of Marine Systems*, 139, 496–504. <https://doi.org/10.1016/j.jmarsys.2014.08.013>
- Campbell, K., Mundy, C., Barber, D., & Gosselin, M. (2015). Characterizing the sea ice algae chlorophyll *a*—Snow depth relationship over Arctic spring melt using transmitted irradiance. *Journal of Marine Systems*, 147, 76–84. <https://doi.org/10.1016/j.jmarsys.2014.01.008>
- Campbell, K., Mundy, C. J., Barber, D. G., & Gosselin, M. (2014). Remote estimates of ice algae biomass and their response to environmental conditions during spring melt. *Arctic*, 67(3), 375. <https://doi.org/10.14430/arctic4409>
- Carnat, G., Zhou, J., Papakyriakou, T., Delille, B., Goossens, T., Haskell, T., Schoemann, V., et al. (2014). Physical and biological controls on DMS, P dynamics in ice shelf-influenced fast ice during a winter-spring and a spring-summer transitions. *Journal of Geophysical Research: Oceans*, 119, 2882–2905. <https://doi.org/10.1002/2013JC009381>
- Castellani, G., Losch, M., Lange, B. A., & Flores, H. (2017). Modeling Arctic sea-ice algae: Physical drivers of spatial distribution and algae phenology. *Journal of Geophysical Research: Oceans*, 122, 7466–7487. <https://doi.org/10.1002/2017JC012828>
- Cimoli, E., Meiners, K. M., Lund-Hansen, L. C., & Lucieer, V. (2018). Spatial variability in sea-ice algal biomass: An under-ice remote sensing perspective. *Advances in Polar Science*, 28(4), 268–296.
- Cota, G. F., & Horne, E. P. (1989). Physical control of arctic ice algal production. *Marine Ecology Progress Series*, 52, 111–121. <https://doi.org/10.3354/meps052111>
- Cota, G. F., Prinsenberg, S. J., Bennett, E. B., Loder, J. W., Lewis, M. R., Anning, J. L., Watson, N. H. F., et al. (1987). Nutrient fluxes during extended blooms of Arctic ice algae. *Journal of Geophysical Research*, 92(C2), 1951–1962. <https://doi.org/10.1029/JC092iC02p01951>
- de Jong, J., Schoemann, V., Maricq, N., Mattioli, N., Langhorne, P., Haskell, T., & Tison, J. L. (2013). Iron in land-fast sea ice of McMurdo Sound derived from sediment resuspension and wind-blown dust attributes to primary productivity in the Ross Sea, Antarctica. *Marine Chemistry*, 157, 24–40. <https://doi.org/10.1016/j.marchem.2013.07.001>
- DeJong, H. B., Dunbar, R. B., Koweeck, D. A., Mucciarone, D. A., Bercovic, S. K., & Hansell, D. A. (2017). Net community production and carbon export during the late summer in the Ross Sea, Antarctica. *Global Biogeochemical Cycles*, 31, 473–491. <https://doi.org/10.1002/2016GB005417>
- DeJong, H. B., Dunbar, R. B., & Lyons, E. A. (2018). Late summer frazil ice-associated algal blooms around Antarctica. *Geophysical Research Letters*, 45, 826–833. <https://doi.org/10.1002/2017GL075472>
- Delille, B., Jourdain, B., Borges, A. V., Tison, J. L., & Delille, D. (2007). Biogas (CO<sub>2</sub>, O<sub>2</sub>, dimethylsulfide) dynamics in spring Antarctic fast ice. *Limnology and Oceanography*, 52(4), 1367–1379. <https://doi.org/10.4319/lo.2007.52.4.1367>
- Delille, D., Fiala, M., Kuparinen, J., Kuosa, H., & Plessis, C. (2002). Seasonal changes in microbial biomass in the first-year ice of the Terre Adélie area (Antarctica). *Aquatic Microbial Ecology*, 28, 257–265. <https://doi.org/10.3354/ame028257>
- Dieckmann, G. S., Arrigo, K., & Sullivan, C. W. (1992). A high-resolution sampler for nutrient and chlorophyll *a* profiles of the sea ice platelet layer and underlying water column below fast ice in polar oceans: Preliminary results. *Marine Ecology Progress Series*, 80, 291–300. <https://doi.org/10.3354/meps080291>
- Dieckmann, G. S., Eicken, H., Haas, C., Garrison, D. L., Gleitz, M., Lange, M., Spindler, M., et al. (1998). A compilation of data on sea ice algal standing crop from the Bellinghausen, Amundsen and Weddell Seas from 1983 to 1994. In M. P. Lizotte, & K. R. Arrigo (Eds.), *Antarctic sea*



- ice: *Biological Processes, Interactions and Variability* (pp. 85–92). Washington, DC: American Geophysical Union. <https://doi.org/10.1029/AR073p0085>
- Drewry, D. J., Jordan, S. R., & Jankowski, E. (1982). Measured properties of the Antarctic ice sheet: Surface configuration, ice thickness, volume and bedrock characteristics. *Annals of Glaciology*, 3, 83–91. <https://doi.org/10.1017/S0260305500002573>
- Eicken, H., Lange, M. A., & Dieckmann, G. S. (1991). Spatial variability of sea-ice properties in the northwestern Weddell Sea. *Journal of Geophysical Research*, 96(C6), 10603–10,615. <https://doi.org/10.1029/91JC00456>
- Evans, C. A., O'Reilly, J. E., & Thomas, J. P. (1987). *A handbook for the measurements of chlorophyll a and primary production, BIOMASS Sci. Ser. 8*. College Station: Tex. A&M Univ.
- Fedotov, V. I., Cherepanov, N. V., & Tyshko, K. P. (1998). Some features of the growth, structure and metamorphism of East Antarctic landfast sea ice. In M. O. Jeffries (Ed.), *Antarctic sea ice: Physical processes, interactions and variability* (pp. 343–354). Washington, DC: American Geophysical Union.
- Feltham, D. L., Worster, M. G., & Wettlaufer, J. S. (2002). The influence of ocean flow on newly forming sea ice. *Journal of Geophysical Research*, 107(C2), 3009. <https://doi.org/10.1029/2000JC000559>
- Fiala, M., Kuosa, H., Kopczyńska, E. E., Oriol, L., & Delille, D. (2006). Spatial and seasonal heterogeneity of sea ice microbial communities in the first-year ice of Terre Adélie area (Antarctica). *Aquatic Microbial Ecology*, 43, 95–106. <https://doi.org/10.3354/ame043095>
- Fraser, A. D., Massom, R. A., Michael, K. J., Galton-Fenzi, B. K., & Lieser, J. L. (2012). East Antarctic landfast sea ice distribution and variability, 2000–08. *Journal of Climate*, 25, 1137–1156.
- Fripiat, F., Sigman, D. M., Massé, G., & Tison, J. L. (2015). High turnover rates indicated by changes in the fixed N forms and their stable isotopes in Antarctic landfast sea ice. *Journal of Geophysical Research: Oceans*, 120, 3079–3097. <https://doi.org/10.1002/2014JC010583>
- Garrison, D. L., & Buck, K. R. (1986). Organism losses during ice melting: A serious bias in sea ice community studies. *Polar Biology*, 6(4), 237–239. <https://doi.org/10.1007/BF00443401>
- Giles, A. B., Massom, R. A., & Lytle, V. I. (2008). Fast-ice distribution in East Antarctica during 1997 and 1999 determined using RADARSAT data. *Journal of Geophysical Research*, 113, C02S14. <https://doi.org/10.1029/2007JC004139>
- Gosselin, M., Legendre, L., Demers, S., & Ingram, R. G. (1985). Responses of sea-ice microalgae to climatic and fortnightly tidal energy inputs (Manitounuk Sound, Hudson Bay). *Canadian Journal of Fisheries and Aquatic Sciences*, 42(5), 999–1006. <https://doi.org/10.1139/f85-125>
- Gough, A. J., Mahoney, A. R., Langhorne, P. J., Williams, M. J., Robinson, N. J., & Haskell, T. G. (2012). Signatures of supercooling: McMurdo Sound platelet ice. *Journal of Glaciology*, 58(207), 38–50. <https://doi.org/10.3189/2012JoG10J218>
- Grossi, S. M., Kottmeier, S. T., Moe, R. L., Taylor, G. T., & Sullivan, C. W. (1987). Sea ice microbial communities. VI. Growth and primary production in bottom ice under graded snow cover. *Marine Ecology Progress Series*, 35, 153–164. <https://doi.org/10.3354/meps035153>
- Grossi, S. M., & Sullivan, C. W. (1985). Sea ice microbial communities. V. The vertical zonation of diatoms in an Antarctic fast ice community. *Journal of Phycology*, 21, 401–409.
- Grotti, M., Soggia, F., Ianni, C., & Frache, R. (2005). Trace metals distributions in coastal sea ice of Terra Nova Bay, Ross Sea, Antarctica. *Antarctic Science*, 17(2), 289–300. <https://doi.org/10.1017/S0954102005002695>
- Günther, S., & Dieckmann, G. S. (1999). Seasonal development of algal biomass in snow-covered fast ice and the underlying platelet layer in the Weddell Sea, Antarctica. *Antarctic Science*, 11(3), 305–315.
- Günther, S., Gleitz, M., & Dieckmann, G. S. (1999). Biogeochemistry of Antarctic sea ice: A case study on platelet ice layers at Drescher inlet, Weddell Sea. *Marine Ecology Progress Series*, 117, 1–13.
- Heil, P., & Allison, I. (2002). Long-term fast-ice variability off Davis and Mawson stations, Antarctica. *Ice in the Environment: Proceedings of the 16th IAHR International Symposium on Ice*, 1, 360–367.
- Heil, P., Allison, I., & Lytle, V. I. (1996). Seasonal and interannual variations of the oceanic heat flux under a landfast Antarctic sea ice cover. *Journal of Geophysical Research*, 101(C11), 25,741–25,752. <https://doi.org/10.1029/96JC01921>
- Heil, P., Gerland, S., & Granskog, M. A. (2011). An Antarctic monitoring initiative for fast ice and comparison with the Arctic. *The Cryosphere Discussion*, 5(5), 2437–2463. <https://doi.org/10.5194/tcd-5-2437-2011>
- Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W., & Strickland, J. D. (1965). Fluorometric determination of chlorophyll. *ICES Journal of Marine Science*, 30(1), 3–15. <https://doi.org/10.1093/icesjms/30.1.3>
- Horne, R., Ackley, S. F., Dieckmann, G. S., Gulliksen, B., Hoshiai, T., Legendre, L., Melnikov, I. A., et al. (1992). Ecology of sea ice biota. *Polar Biology*, 12, 417–427.
- Hoshiai, T. (1972). Diatom distribution in sea ice near McMurdo and Syowa Stations. *Antarctic Journal of the United States*, 7, 84.
- Hoshiai, T. (1977). Seasonal change of ice communities in the sea ice near Syowa Station Antarctica. In M. J. Dunbar (Ed.), *Polar oceans*, (pp. 307–317). Calgary: Arctic Institute of North America.
- Hoshiai, T. (1981). The plant pigments, chlorinity and pH distribution in the sea ice of the Syowa station area in 1970. *Japanese Antarctic Research Expeditions Data Report (Marine Biology)*, 67, 1–42.
- Kohlbach, D., Graeve, M., Lange, B. A., David, C., Schaafsma, F. L., van Franeker, J. A., Vorkamp, M., et al. (2018). Dependency of Antarctic zooplankton species on ice algae-produced carbon suggests a sea ice-driven pelagic ecosystem during winter. *Global Change Biology*, 24(10), 4667–4681. <https://doi.org/10.1111/gcb.14392>
- Kohlbach, D., Lange, B., Schaafsma, F., David, C., Vorkamp, M., Graeve, M., van Franeker, J. A., et al. (2017). Ice algae-produced carbon is critical for overwintering of Antarctic krill *Euphausia superba*. *Frontiers in Marine Science*, 4, 1–16. <https://doi.org/10.3389/fmars.2017.00310>
- Krembs, C., Gradinger, R., & Spindler, M. (2000). Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. *Journal of Experimental Marine Biology and Ecology*, 243(1), 55–80. [https://doi.org/10.1016/S0022-0981\(99\)00111-2](https://doi.org/10.1016/S0022-0981(99)00111-2)
- Lange, B. A., Katlein, C., Castellani, G., Fernandez-Mendez, M., Nicolaus, M., Peeken, I., & Flores, H. (2017). Characterizing spatial variability of ice algal chlorophyll a and net primary production between sea ice habitats using horizontal profiling platforms. *Frontiers in Marine Science* <https://doi.org/10.3389/fmars.2017.00349>, 4, 1–23.
- Lange, B. A., Katlein, C., Nicolaus, M., Peeken, I., & Flores, H. (2016). Sea ice algae chlorophyll a concentrations derived from under-ice spectral radiation profiling platforms. *Journal of Geophysical Research: Oceans*, 121, 8511–8534. <https://doi.org/10.1002/2016JC011991>
- Lange, B. A., Michel, C., Beckers, J. F., Casey, J. A., Flores, H., Hatam, I., Meisterhans, G., et al. (2015). Comparing springtime ice-algal chlorophyll a and physical properties of multi-year and first-year sea ice from the Lincoln Sea. *PLoS One*, 10(4), e0122418. <https://doi.org/10.1371/journal.pone.0122418>
- Langhorne, P. J., Hughes, K. G., Gough, A. J., Smith, I. J., Williams, M. J. M., Robinson, N. J., Stevens, C. L., et al. (2015). Observed platelet ice distributions in Antarctic sea ice: An index for ocean-ice shelf heat flux. *Geophysical Research Letters*, 42, 5442–5451. <https://doi.org/10.1002/2015GL064508>
- Lannuzel, D., van der Merwe, P. C., Townsend, A. T., & Bowie, A. R. (2014). Size fractionation of iron, manganese and aluminium in Antarctic fast ice reveals a lithogenic origin and low iron solubility. *Marine Chemistry*, 161, 47–56. <https://doi.org/10.1016/j.marchem.2014.02.006>

- Leonard, G. H., Purdie, C. R., Langhorne, P. J., Haskell, T. G., Williams, M. J. M., & Frew, R. D. (2006). Observations of platelet ice growth and oceanographic conditions during the winter of 2003 in McMurdo Sound, Antarctica. *Journal of Geophysical Research*, 111, C04012. <https://doi.org/10.1029/2005JCC002952>
- Leu, E., Mundy, C. J., Assmy, P., Campbell, K., Gabrielsen, T. M., Gosselin, M., Juul-Pedersen, T., et al. (2015). Arctic spring awakening—Steering principles behind the phenology of vernal ice algal blooms. *Progress in Oceanography*, 139, 151–170. <https://doi.org/10.1016/j.pcean.2015.07.012>
- Lieser, J. L., Curran, M. A. J., Bowie, A. R., Davidson, A. T., Doust, S. J., Fraser, A. D., Galton-Fenzi, B. K., et al. (2015). Antarctic slush-ice algal accumulation not quantified through conventional satellite imagery: Beware the ice of March. *The Cryosphere Discuss*, 9, 6187–6222. <https://doi.org/10.5194/tcd-9-6187-2015>
- Maksym, T., & Markus, T. (2008). Antarctic sea ice thickness and snow-to-ice conversion from atmospheric reanalysis and passive microwave snow depth. *Journal of Geophysical Research*, 113, C02S12. <https://doi.org/10.1029/2006JC004085>
- Massom, R. A., Hill, K. L., Lytle, V. I., Worby, A. P., Paget, M. J., & Allison, I. (2001). Effects of regional fast-ice and iceberg distributions on the behaviour of the Mertz Glacier polynya, East Antarctica. *Annals of Glaciology*, 33, 391–398. <https://doi.org/10.3189/172756401781818518>
- McConville, M. J., Mitchell, C., & Wetherbee, R. (1985). Patterns of carbon assimilation in a microalgal community from annual sea ice, East Antarctica. *Polar Biology*, 4(3), 135–141. <https://doi.org/10.1007/BF00263876>
- McConville, M. J., & Wetherbee, R. (1983). The bottom-ice microalgal community from annual ice in the inshore waters of East Antarctica. *Journal of Phycology*, 19(4), 431–439. <https://doi.org/10.1111/j.0022-3646.1983.00431.x>
- McMinn, A., Ashworth, C., & Ryan, K. G. (2000). *In situ* net primary productivity of an Antarctic fast ice bottom algal community. *Aquatic Microbial Ecology*, 21, 177–185. <https://doi.org/10.3354/ame021177>
- McMinn, A., Martin, A., & Ryan, K. (2010). Phytoplankton and sea ice algal biomass and physiology during the transition between winter and spring (McMurdo Sound, Antarctica). *Polar Biology*, 33(11), 1547–1556. <https://doi.org/10.1007/s00300-010-0844-6>
- McMinn, A., Pankowskii, A., Ashworth, C., Bhagooli, R., Ralph, P., & Ryan, K. (2010). *In situ* net primary productivity and photosynthesis of Antarctic sea ice algal, phytoplankton and benthic algal communities. *Marine Biology*, 157(6), 1345–1356. <https://doi.org/10.1007/s00227-010-1414-8>
- McMinn, A., Skerratt, J., Trull, T., Ashworth, C., & Lizotte, M. (1999). Nutrient stress gradient in the bottom 5 cm of fast ice, McMurdo Sound, Antarctica. *Polar Biology*, 21(4), 220–227. <https://doi.org/10.1007/s003000050356>
- McMullin, R. M., Wing, S. R., Wing, L. C., & Shatova, O. A. (2017). Trophic position of Antarctic ice fishes reflects food web structure along a gradient in sea ice persistence. *Marine Ecology Progress Series*, 564, 87–98. <https://doi.org/10.3354/meps12031>
- Meiners, K. M., Arndt, S., Bestley, S., Krumpen, T., Ricker, R., Milnes, M., Newbery, K., et al. (2017). Antarctic pack-ice algal distribution: Floe-scale spatial variability and predictability from physical parameters. *Geophysical Research Letters*, 44, 7382–7390. <https://doi.org/10.1002/2017GL074346>
- Meiners, K. M., & Michel, C. (2017). Dynamics of nutrients, dissolved organic matter and exopolymers in sea ice. In D. N. Thomas (Ed.), *Sea ice* (pp. 415–432). Hoboken, NJ: John Wiley. <https://doi.org/10.1002/9781118778371.ch17>
- Meiners, K. M., Vancoppenolle, M., Thanassekos, S., Dieckmann, G. S., Thomas, D. N., Tison, J. L., Arrigo, K. R., et al. (2012). Chlorophyll *a* in Antarctic sea ice from historical ice core data. *Geophysical Research Letters*, 39, L21602. <https://doi.org/10.1029/2012GL053478>
- Melbourne-Thomas, J., Meiners, K. M., Mundy, C. J., Schallenberg, C., Tattersall, K. L., & Dieckmann, G. S. (2015). Algorithms to estimate Antarctic sea ice algal biomass from under-ice irradiance spectra at regional scales. *Marine Ecology Progress Series*, 536, 107–121. <https://doi.org/10.3354/meps11396>
- Miller, L. A., Fripiat, F., Else, B. G. T., Bowman, J. S., Brown, K. A., Collins, R. E., Ewert, M., et al. (2015). Methods for biogeochemical studies of sea ice: The state of the art, caveats, and recommendations. *Elementa-Oceans*, 3, 1–53. <https://doi.org/10.12952/journal.elementa.000038>
- Mundy, C. J., Barber, D. G., & Michel, C. (2005). Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. *Journal of Marine Systems*, 58(3–4), 107–120. <https://doi.org/10.1016/j.jmarsys.2005.07.003>
- Nicolaus, M., Hudson, S. R., Gerland, S., & Munderloh, K. (2010). A modern concept for autonomous and continuous measurements of spectral albedo and transmittance of sea ice. *Cold Regions Science and Technology*, 62(1), 14–28. <https://doi.org/10.1016/j.coldregions.2010.03.001>
- Niemi, A., Michel, C., Hille, K., & Poulin, M. (2011). Protist assemblages in winter sea ice: Setting the stage for the spring ice algal bloom. *Polar Biology*, 34(12), 1803–1817. <https://doi.org/10.1007/s00300-011-1059-1>
- Nihashi, S., & Ohshima, K. I. (2015). Circumpolar mapping of Antarctic coastal polynyas and landfast sea ice: Relationship and variability. *Journal of Climate*, 28(9), 3650–3670. <https://doi.org/10.1175/JCLI-D-14-00369.1>
- Nomura, D., Kasamatsu, N., Tateyama, K., Kudoh, S., & Fukuchi, M. (2011). DMSP and DMS in coastal fast ice and under-ice water of Lützow-Holm Bay, Eastern Antarctica. *Continental Shelf Research*, 31, 1377–1383.
- Perovich, D. K. (2017). Sea ice and sunlight. In D. N. Thomas (Ed.), *Sea ice*, (pp. 110–137). Hoboken, NJ, John Wiley. <https://doi.org/10.1002/9781118778371.ch4>
- Remy, J. P., Becquevort, S., Haskell, T. G., & Tison, J. L. (2008). Impact of the B-15 iceberg “stranding event” on the physical and biological properties of sea ice in McMurdo Sound, Ross Sea, Antarctica. *Antarctic Science*, 20(06), 593–604. <https://doi.org/10.1017/S0954102008001284>
- Rintala, J. M., Piiparinen, J., Blomster, J., Majaneva, M., Müller, S., Uusikivi, J., & Autio, R. (2014). Fast direct melting of brackish sea-ice samples results in biologically more accurate results than slow buffered melting. *Polar Biology*, 37(12), 1811–1822. <https://doi.org/10.1007/s00300-014-1563-1>
- Robinson, D. H., Arrigo, K. R., Kolber, Z., Gosselin, M., & Sullivan, C. W. (1998). Photophysiological evidence of nutrient limitation of platelet ice algae in McMurdo Sound, Antarctica. *Journal of Phycology*, 34(5), 788–797. <https://doi.org/10.1046/j.1529-8817.1998.340788>
- Schaafsma, F. L., Kohlbach, D., David, C., Lange, B. A., Graeve, M., Flores, H., & van Franeker, J. (2017). Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill, *Euphausia superba*, in ice-covered waters. *Marine Ecology Progress Series*, 580, 101–115. <https://doi.org/10.3354/meps12309>
- Schmidt, K., Brown, T. A., Belt, S. T., Ireland, L. C., Taylor, K. W. R., Thorpe, S. E., Ward, P., et al. (2018). Do pelagic grazers benefit from sea ice? Insights from the Antarctic sea ice proxy IPSO<sub>25</sub>. *Biogeosciences*, 15(7), 1987–2006. <https://doi.org/10.5194/bg-15-1987-2018>
- Shine, K. P. (1984). Parametrization of the shortwave flux over high albedo surfaces as a function of cloud thickness and surface albedo. *Quarterly Journal of the Royal Meteorological Society*, 110(465), 747–764. <https://doi.org/10.1002/qj.49711046511>
- Smetacek, V., Scharek, R., Gordon, L. I., Eicken, H., Fahrback, E., Rohardt, G., & Moore, S. (1992). Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea, Antarctica. *Deep Sea Research Part A: Oceanographic Research Papers*, 39(2), 153–168. [https://doi.org/10.1016/0198-0149\(92\)90102-Y](https://doi.org/10.1016/0198-0149(92)90102-Y)
- Smith, I. J., Langhorne, P. J., Haskell, T. G., Trodahl, H. J., Frew, R., & Ross Vennell, M. (2001). Platelet ice and the land-fast sea ice of McMurdo Sound, Antarctica. *Annals of Glaciology*, 33, 21–27. <https://doi.org/10.3189/172756401781818365>

- Stoecker, D. K., Gustafson, D. E., Black, M., & Baier, C. T. (1998). Population dynamics of microalgae in the upper land-fast sea ice at a snow-free location. *Journal of Phycology*, 34(1), 60–69. <https://doi.org/10.1046/j.1529-8817.1998.340060.x>
- Sturm, M., & Massom, R. A. (2017). Snow in the sea ice system: Friend or foe? In D. N. Thomas (Ed.), *Sea ice* (pp. 65–109). Hoboken, NJ: John Wiley. <https://doi.org/10.1002/9781118778371.ch3>
- Swadling, K. M., McKinnon, A. D., De'ath, G., & Gibson, J. A. E. (2004). Life cycle plasticity and differential growth and development in marine and lacustrine populations of an Antarctic copepod. *Limnology and Oceanography*, 49(3), 644–655. <https://doi.org/10.4319/lo.2004.49.3.0644>
- Swadling, K. M., McPhee, A. D., & McMinn, A. (2000). Spatial distribution of copepods in fast ice of eastern Antarctica. *Polar Bioscience*, 13, 55–65.
- Tison, J. L., Delille, B., & Papadimitriou, S. (2017). Gases in sea ice. In D. N. Thomas (Ed.), *Sea ice* (pp. 433–471). Hoboken, NJ: John Wiley. <https://doi.org/10.1002/9781118778371.ch18>
- Tison, J. L., Schwegmann, S., Dieckmann, G., Rintala, J. M., Meyer, H., Moreau, S., Vancoppenolle, M., et al. (2017). Biogeochemical impact of snow cover and cyclonic intrusions on the winter Weddell Sea ice pack. *Journal of Geophysical Research: Oceans*, 122, 9548–9571. <https://doi.org/10.1002/2017JC013288>
- Ushio, S. (2006). Factors affecting fast-ice break-up frequency in Lützow-Holm Bay, Antarctica. *Annals of Glaciology*, 44, 177–182. <https://doi.org/10.3189/172756406781811835>
- van der Merwe, P., Lannuzel, D., Bowie, A. R., & Meiners, K. M. (2011). High temporal resolution observations of spring fast ice melt and seawater iron enrichment in East Antarctica. *Journal of Geophysical Research*, 116, G03017. <https://doi.org/10.1029/2010JG001628>
- van der Merwe, P., Lannuzel, D., Mancuso Nichols, C., Meiners, K. M., Heil, P., et al. (2009). Biogeochemical observations during the winter-spring transition in East Antarctic sea ice: Evidence of iron and exopolysaccharide controls. *Marine Chemistry*, 115(3–4), 163–175. <https://doi.org/10.1016/j.marchem.2009.08.001>
- van Leeuwe, M. A., Tedesco, L., Arrigo, K. R., Assmy, P., Campbell, K., Meiners, K. M., Rintala, J. M., et al. (2018). Microalgal community structure and primary production in Arctic and Antarctic sea ice: A synthesis. *Elementa: Oceans*, 6, 1–25. <https://doi.org/10.1525/elementa.267>
- van Leeuwe, M. A., Villerius, L. A., Roggevel, J., Visser, R. J. W., & Stefels, J. (2006). An optimized method for automated analysis of algal pigments by HPLC. *Marine Chemistry*, 102(3–4), 267–275. <https://doi.org/10.1016/j.marchem.2006.05.003>
- Vancoppenolle, M. (2017, Updated 2018). The BEPSII sea ice core analyser. (<https://pagesperso.icean-ipsl.upmc.fr/mvloed/>).
- Vancoppenolle, M., Meiners, K. M., Michel, C., Bopp, L., Brabant, F., Carnat, G., Delille, B., et al. (2013). Role of sea ice in global biogeochemical cycles: Emerging views and challenges. *Quaternary Science Reviews*, 79, 207–230. <https://doi.org/10.1016/j.quascirev.2013.04.011>
- Vermeulen, F. A. H. (2013). The influences of nutrients and snow on the spatial and temporal variability of sea ice algae, PhD Thesis, Victoria University of Wellington, New Zealand, pp. 1–165, <http://hdl.handle.net/10063/2940>
- Watanabe, K., Satoh, H., Takahashi, E., & Kanda, H. (1990). Pigment data of sea ice cores collected from fast ice area near Syowa station, Antarctica, from March 1983 to January 1984 (JARE 24). *Japanese Antarctic Research Expeditions Data Report (Marine Biology)*, 16, 1–88.
- Welch, H. E., & Bergman, M. A. (1989). Seasonal development of ice algae and its prediction from environmental factors near Resolute, N.W.T., Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 1973–1804.
- Whitaker, T. M., & Richardson, M. G. (1980). Morphology and chemical composition of a natural population of an ice-associated Antarctic diatom *Navicula glaciei*. *Journal of Phycology*, 16(2), 250–257. <https://doi.org/10.1111/j.1529-8817.1980.tb03027.x>
- Wing, S. R., McLeod, R. J., Leichter, J. J., Frew, R. D., & Lamare, M. D. (2012). Sea ice microbial production supports Ross Sea benthic communities: Influence of a small but stable subsidy. *Ecology*, 93(3), 14–323.
- Wongpan, P., Meiners, K. M., Langhorne, P. J., Heil, P., Smith, I. J., Leonard, G. H., Massom, R. A., et al. (2018). Estimation of Antarctic land-fast sea ice algal biomass and snow thickness from under-ice radiance spectra in two contrasting areas. *Journal of Geophysical Research: Oceans*, 123, 1907–1923. <https://doi.org/10.1002/2017JC013711>
- Worby, A. P., Geiger, C. A., Paget, M. J., Van Woert, M. L., Ackley, S. F., & DeLiberty, T. L. (2008). Thickness distribution of Antarctic sea ice. *Journal of Geophysical Research*, 113, C05S92. <https://doi.org/10.1029/2007JC004254>
- World Meteorological Organization (1970). WMO sea-ice nomenclature. Terminology, codes and illustrated glossary. *Geneva Secretariat of the World Meteorological Organization Technical Report*, 259, 1–147.